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The influence of air pollution on moss-dwelling animals: 4. Seasonal and long-term fluctuations of rotifer, nematode and tardigrade populations

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The influence of air pollution on moss-dwelling animals: 4. Seasonal and long-term fluctuations of rotifer, nematode and tardigrade population. – The variation of moss-dwelling aquatic communities was studied at two microsites over a period of seven years. Nematodes and tardigrades were identified to the species level; rotifers were treated as a group. Seasonal trends in population fluctuations were investigated between August 1983 and March 1985. The long-term pattern was examined by sampling between March 1984 and March 1989 at yearly intervals. Species richness and abundance were considerably greater for nematodes than for tardigrades. The seasonal abundance pattern of nematodes and tardigrades showed a peak in May and a population low in November and March. The long-term fluctuations of tardigrade numbers showed a peak in 1987 with a minimal abundance in 1989. Nematode numbers at one microsite fluctuated similarly to tardigrade numbers, while the abundance of nematodes at the other microsite was relatively stable. Despite pronounced quantitative changes, the qualitative composition of nematode and tardigrade communities was considerably stable throughout the study period.

Key-words: Nematoda – Tardigrada – Moss-invertebrate associations – Seasonal fluctuations – Long-term fluctuations – Stability.

INTRODUCTION

Moss-dwelling nematode and tardigrade communities respond sensitively to changes in air quality (Steiner, 1994a, b, 1995b). Since the aquatic fauna of moss cushions is closely related to the soil fauna (Nicholas, 1984), it could act as an indicator system of air pollution effects on soil ecosystems. Ecological monitoring, however, presupposes that the indicator communities remain relatively stable under normal fluctuations in environmental conditions.

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Only two studies deal with the dynamics of moss-inhabiting invertebrates. ZULLINI (1971) and MORGAN (1977) investigated seasonal changes of nematode and tardigrade populations, respectively. There is no study known to the author concerning the long-term variation of moss-dwelling nematode and tardigrade communities. The present study was designed to investigate the qualitative and quantitative variation of the moss-inhabiting aquatic fauna over several generations.

MATERIAL AND METHODS

1. DESCRIPTION OF THE STUDY SITE

The study was conducted at an intermediately polluted urban site (site "Dyn"; see STEINER, 1994a) situated close to the center of Zürich (430m asl). The samples were taken from a sunken sandstone wall covered by large moss cushions of *Homalothecium* cf. *sericeum* (Hedw.) B.S.G. and located ten meters away from a frequented road. In the collecting area, two microsites (area 1 and area 2) of about 0.25 m^2 each were repeatedly sampled between 1982 and 1989. They were located two meters apart and were separated by a little projection in the wall. No visible changes of the moss cover were observed throughout the study. Annual mean levels of air pollution were assumed to be constant over the observation period. Evidence is given by the constant traffic volume and permanent air pollution measurements at a nearby recording site. The climate is typical of the Northern Temperate Zone with warm summers (average air temperature in July: 17 °C) and cool winters (January: -1 °C). Meteorological data were recorded at a nearby station (Schweizerische Meteorologische Anstalt, Krähbühlstr. 58, 8044 Zürich).

2. SAMPLE COLLECTION AND PROCESSING

At each sampling date, five sampling units (cores of ca. 1 cm^2 each) were taken from each microsite along a horizontal transect. A cylindrical steel corer (diameter = 11 mm) was used. Generally the five sampling units from one microsite were then pooled to constitute a sample of 5 cm^2. The variation in nematode and tardigrade numbers within sampling units of a sample was determined in August 1982 (six preliminary samples), August 1983 and March 1989 (two samples each). Analysis of seasonal community changes (species richness and abundance) is based on 16 samples taken between August 1983 and March 1985. Intervals between samplings were two months, but no samples were taken between November and March. The long-term pattern was examined by sampling every March between 1984 and 1989 (12 samples). The data for March 1984 and March 1985 were used in the study of both seasonal and long-term population fluctuations.

The fauna was extracted using a modified version of Oostenbrink's funnel-spray method. A complete description of the methods for processing the fauna is given by STEINER (1994a). Due to low numbers of extracted microarthropods, the present paper deals only with the moss-dwelling aquatic fauna. Nematodes and tardigrades were identified to the species level; rotifers were treated as a group. For taxonomic comments and a complete species list (including the microarthropods) see STEINER (1994a).

RESULTS

A total of 10'935 nematodes (relative abundance 67%, 23 taxa), 2'215 tardigrades (13%, seven species), and 3'140 rotifers (20%) was collected. The overall density of aquatic animals was 133 ± 93 individuals/cm^2 (mean ± standard deviation, n = 24), with nematodes occurring at higher numbers than both rotifers and tardigrades (sign test, $p < 0.001$).

1. ACCURACY OF POPULATION ESTIMATES

For the main taxa and the most common species the mean (n = 10) accuracy of abundance estimates is indicated in tab. 1. The coefficients of variation of the taxa rotifers, nematodes and tardigrades ranged between 21 - 56%, 14 - 46% and 7 - 76%, respectively, and were higher in 1989 than in 1983. At the species level, the mean accuracy of population estimates was generally lower than for main taxa (tab. 1). It is concluded that the seasonal abundance patterns of main taxa (figs 1 and 6) reflect true changes in abundance, whereas the long-term abundance patterns, as well as population changes of single species, must be interpreted with care.

TAB. 1.

Variation coefficients of rotifer, nematode and tardigrade numbers within sampling units of a sample (cv = average coefficient of variation, n = 10, samples with ≤ 5 individuals of a given taxon were excluded).

Taxa	cv
Rotifers	36
Nematodes	25
Aphelenchoides sp. 5	52
Geomonhystera villosa	41
Plectus cf. *parietinus*	68
Plectus parvus	43
Chiloplectus cf. *andrassyi*	48
Tylocephalus auriculatus	55
Paratripyla intermedia	42
Tardigrades	42
Macrobiotus persimilis	39
Hypsibius oberhaeuseri	48

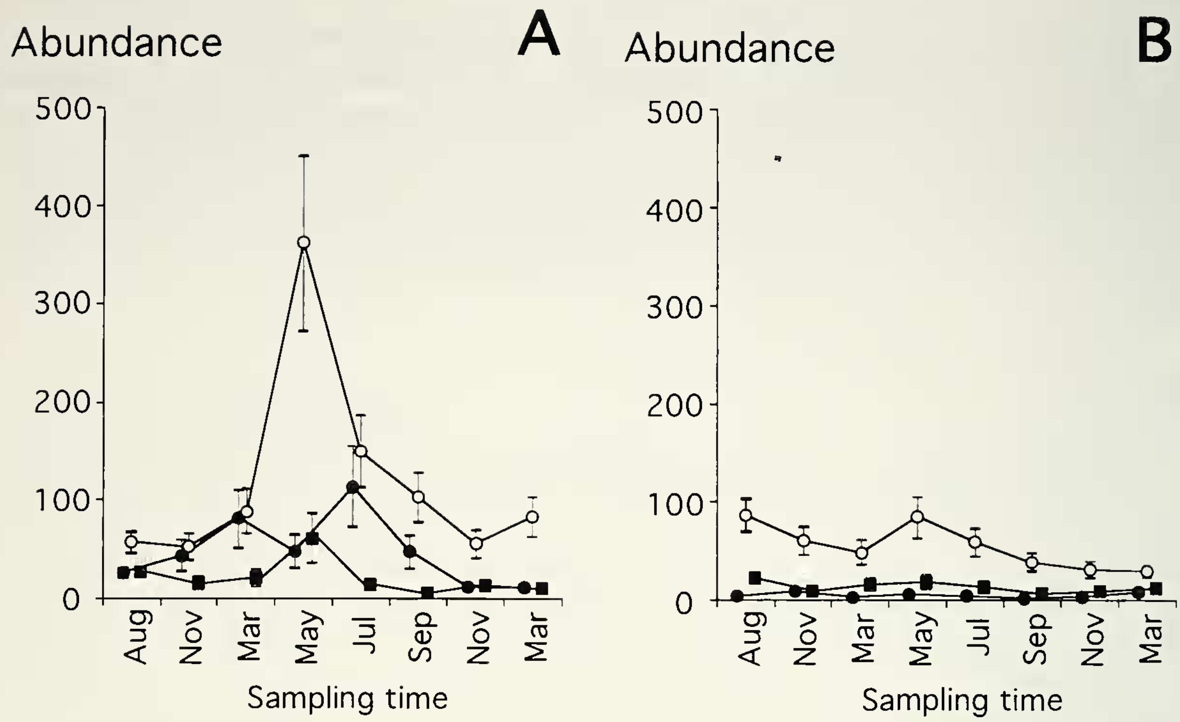

FIG. 1.

Seasonal changes in the abundance (individuals/cm^2; average ± standard error) of moss-dwelling rotifers, nematodes and tardigrades in area 1 (A) and area 2 (B). Samples were taken between August 1983 and March 1985. Error bars (except August) denote estimated standard errors based on values given in tab. 1 (rotifers: ● nematodes: ○; tardigrades: ■).

2. Seasonal variation in the abundances of higher taxonomic categories

As indicated in fig. 1, the seasonal changes of all taxa were more pronounced in area 1 than in area 2. Nematodes dominated quantitatively. While rotifer numbers were significantly higher in area 1 than in area 2 (Mann-Whitney U-test, $p < 0.001$), there was no significant difference for total nematodes and tardigrades. Both taxa reached a maximum in May 1984, with a similar abundance pattern of tardigrades at both microsites ($r_s = 0.81$, $p < 0.05$; see also fig. 4).

Visual examination of fig. 2 suggests that nematode and tardigrade numbers are negatively related to temperature. Their abundance tended to increase below a limit of about 10 °C. No significant relationship was found between the abundance of predatory species and the remaining taxa.

3. Seasonal variation in species composition

Nematodes

The qualitative composition of nematode communities is similar at both microsites. Of the 23 nematode taxa recorded at study site "Dyn" (see STEINER, 1994a), 19 (83%) were found in area 1, only 14 (61%) in area 2. Twelve species are common to

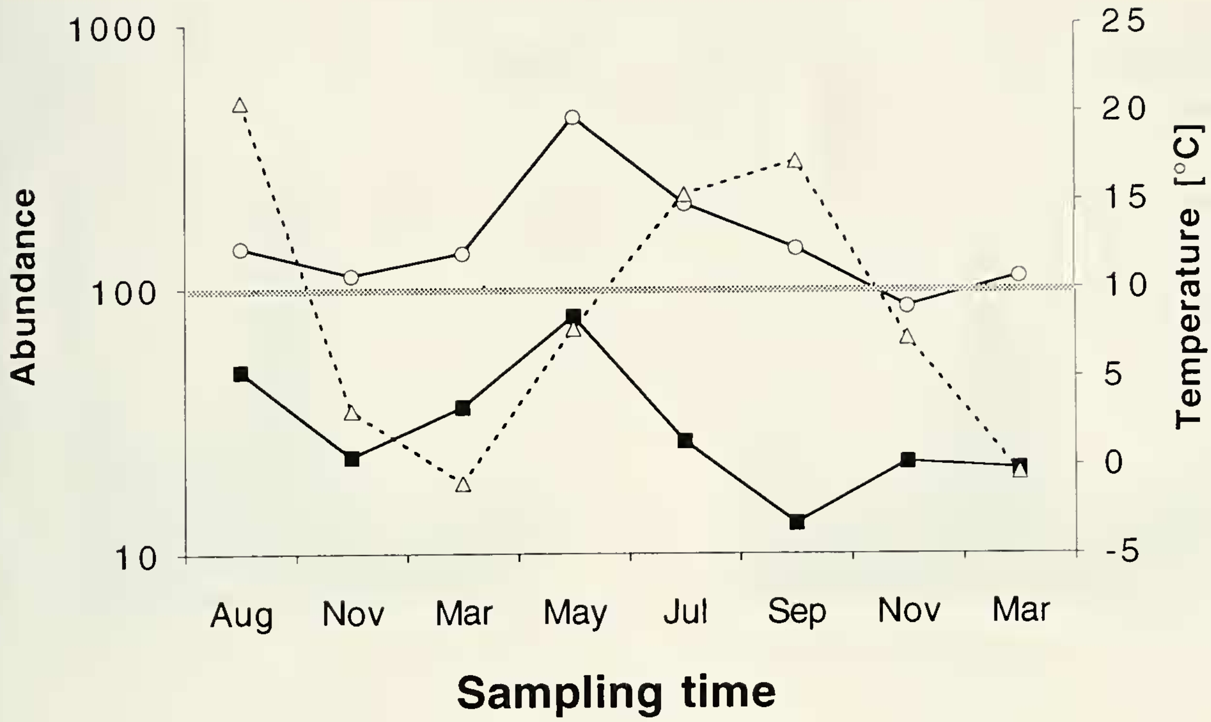

FIG. 2

Seasonal changes in temperature (average temperature 30 d prior to sampling) and in the abundance (individuals/cm^2) of moss-dwelling nematodes and tardigrades (temperature: Δ; nematodes: □; tardigrades: ■).

both areas. *Geomonhystera villosa* (Bütschli), Plectidae sp. (predominantly unidentified first larval instars), *Plectus* cf. *parietinus* Bastian, *Chiloplectus* cf. *andrassyi* (Timm) and *Paratripyla intermedia* (Bütschli) occurred in all the samples. *Aphelenchoides* sp. 5, *Plectus parvus* Bastian, *Tylocephalus auriculatus* (Bütschli) and Dorylaimidae were other characteristic taxa of area 1 and/or area 2.

The population size of several taxa increased between March and May 1984, followed by a gradual decline until November 1984 (fig. 3). The most pronounced seasonal pattern was observed for the taxon Plectidae sp. (both areas) and for *Aphelenchoides* sp. 5 (area 2). The quickly swelling abundance of the Plectidae sp. between March and May 1984 indicates high reproduction in spring. The subsequent, relatively large populations of *P.* cf. *parietinus* (fig. 3A) and *C.* cf. *andrassyi* (fig. 3B) can be explained by transition of first larval instars to later stages, that could then be identified to the species level.

Tardigrades

The seasonal variation of tardigrade populations is shown in fig. 4. Species composition at both microsites was considerably stable through time. Despite the more pronounced tardigrade peak in area 1, only small differences exist between the two microsites. All the seven species of the study site "Dyn" were found in area 1, including

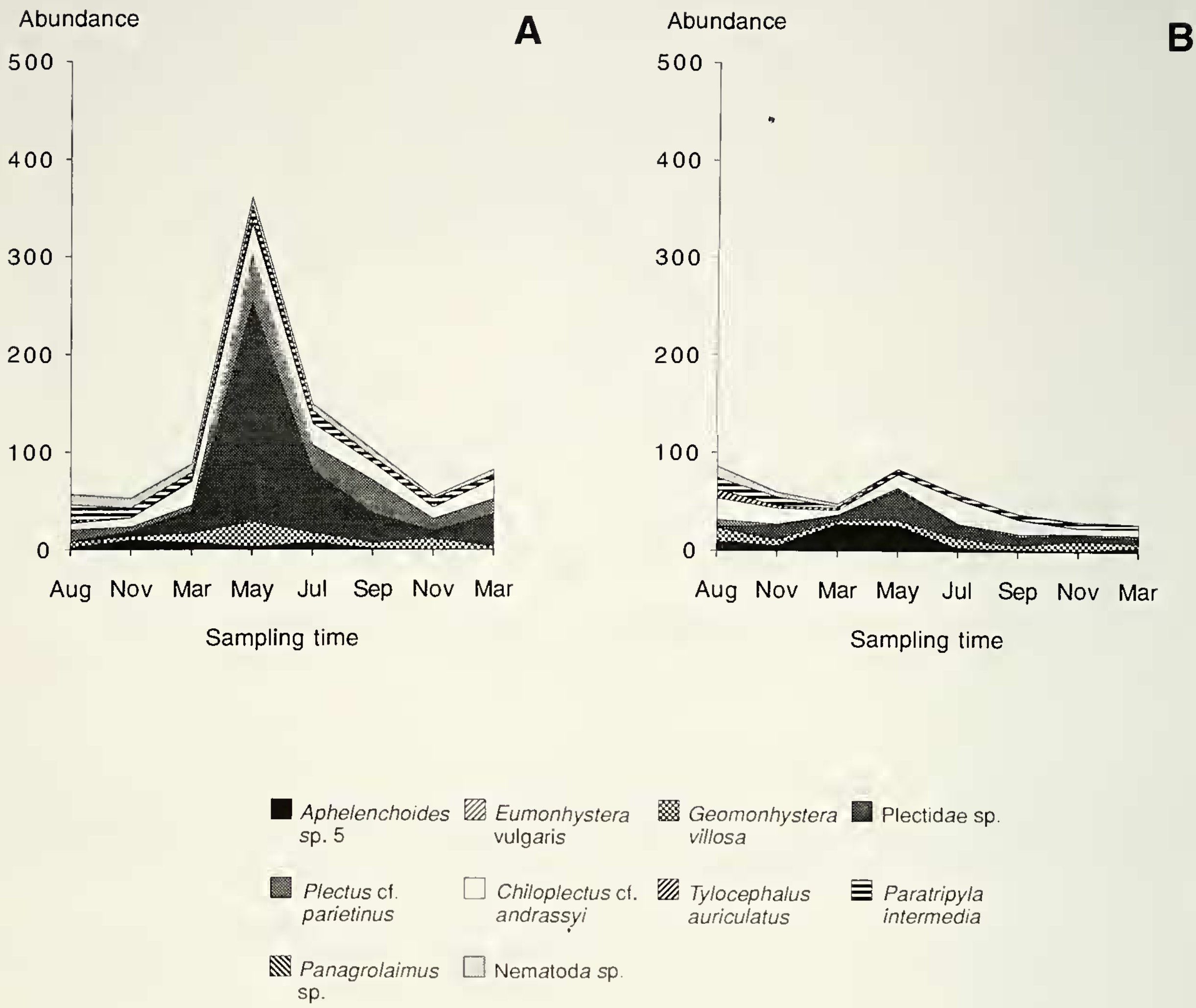

FIG. 3

Seasonal changes in the abundance (individuals/cm^2) of moss-dwelling nematode taxa in area 1 (A) and area 2 (B). Samples were taken between August 1983 and March 1985. Rare species were placed in the taxon Nematoda sp.

the five species detected in area 2. *Macrobiotus richtersi* Murray and *Isohypsibius prosostomus* (Thulin) occurred exclusively in area 1. Dominant species were *Macrobiotus persimilis* Binda & Pilato and *Hypsibius oberhaeuseri* (Doyère) which were present at all sampling dates (fig. 4) and accounted for 83% of the total extracted tardigrades. Densities of other species were generally low throughout the year. The high abundances of *M. persimilis* and *H. oberhaeuseri* in May 1984 coincided with the peak in nematode numbers, indicating favorable conditions for both taxa in late spring. Populations of *M. persimilis* always decreased in summer (July to September), followed by increasing densities in autumn. The moderate peak of *M. hufelandi* (Schultze) discernible in summer agrees with findings of MORGAN (1977).

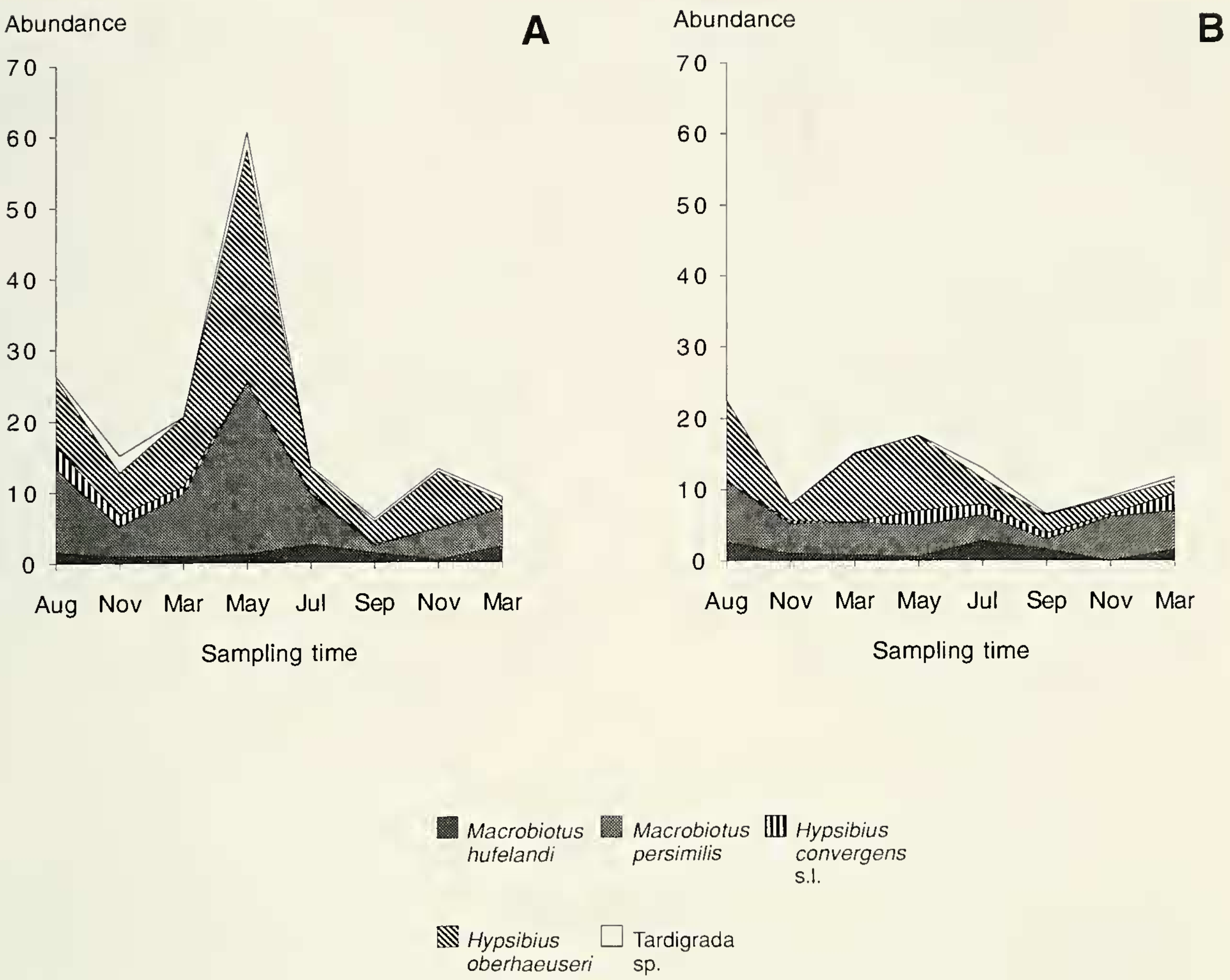

FIG. 4

Seasonal changes in the abundance (individuals/cm^2) of moss-dwelling tardigrade taxa in area 1 (A) and area 2 (B). Samples were taken between August 1983 and March 1985. Rare species were placed in the taxon Tardigrada sp.

4. SEASONAL VARIATION IN SPECIES RICHNESS

The temporal stability in the species composition of the aquatic community (chapter Results, section 3) is also expressed in approximately stable species numbers (fig. 5). Nematode communities were richer in species than tardigrade communities. More nematode species were always detected in area 1, while the number of tardigrade species was similar in both areas. Surprisingly, the curve patterns of species numbers (fig. 5) and abundances (fig. 1) are divergent. Maximum species counts were made in November 1983 and March 1984, as well as in September and November 1984, when the abundances were relatively low.

As compared with total species richness, the mean number of nematode species detected per sampling occasion (11.5 or 61% in area 1, and 8.8 or 68% in area 2) was relatively low. For tardigrades, the corresponding values were higher (4.8 or 69%, and

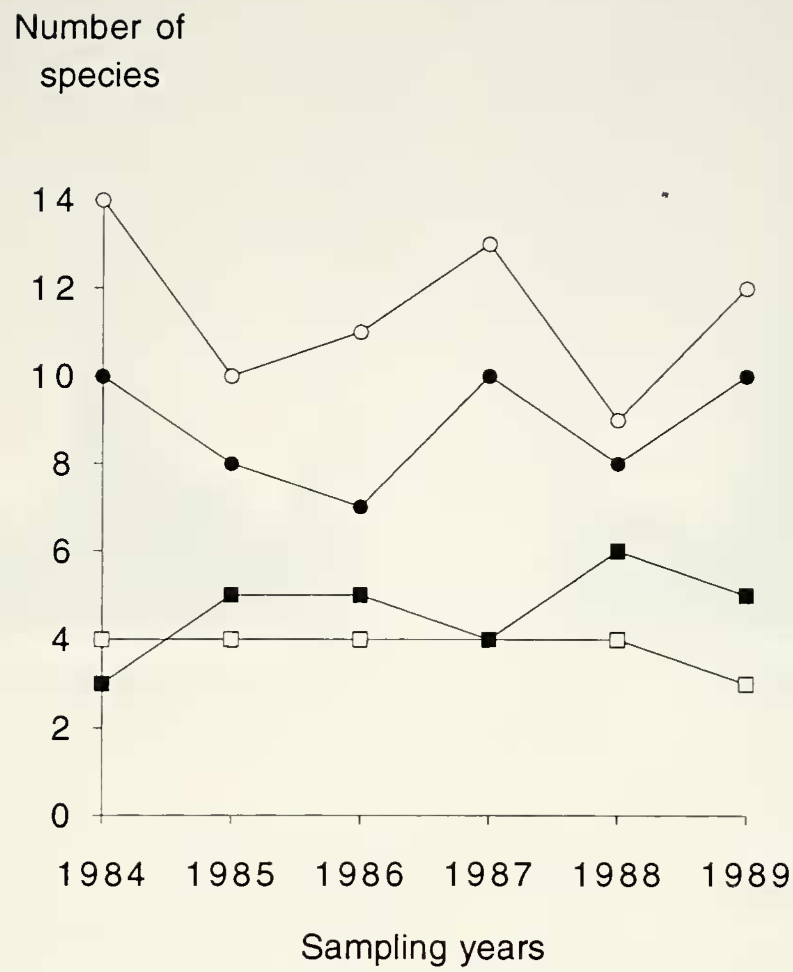

Fig. 5

Seasonal changes in species richness of moss-dwelling nematodes and tardigrades in area 1 and area 2. Samples were taken between August 1983 and March 1985 (nematodes: ○ area 1, ● area 2; tardigrades: □ area 1, ■ area 2).

4.0 or 80%). This confirms the assumption that moss-dwelling tardigrade species are more evenly distributed than nematode species (Steiner, 1990).

5. Long-term variation in the abundances of higher taxonomic categories

The abundances of rotifers, nematodes and tardigrades measured at yearly intervals from 1984 to 1989 are given in fig. 6. Common characteristics of all three taxa are a slight depression in 1985 and a relatively sharp decrease in numbers between 1988 and 1989. Nematodes dominated in all samples.

Rotifer numbers in area 2 exhibited the most pronounced long-term variation (fig. 6B). In all the samples between August 1983 and March 1986, the abundance of rotifers was consistently low (see also fig. 1B). Thereon, it increased continuously, culminating in a peak in March 1988. In area 1 the abundance of rotifers fluctuated irregularly. Until 1986 they were more abundant in area 1 than in area 2 (see also fig.

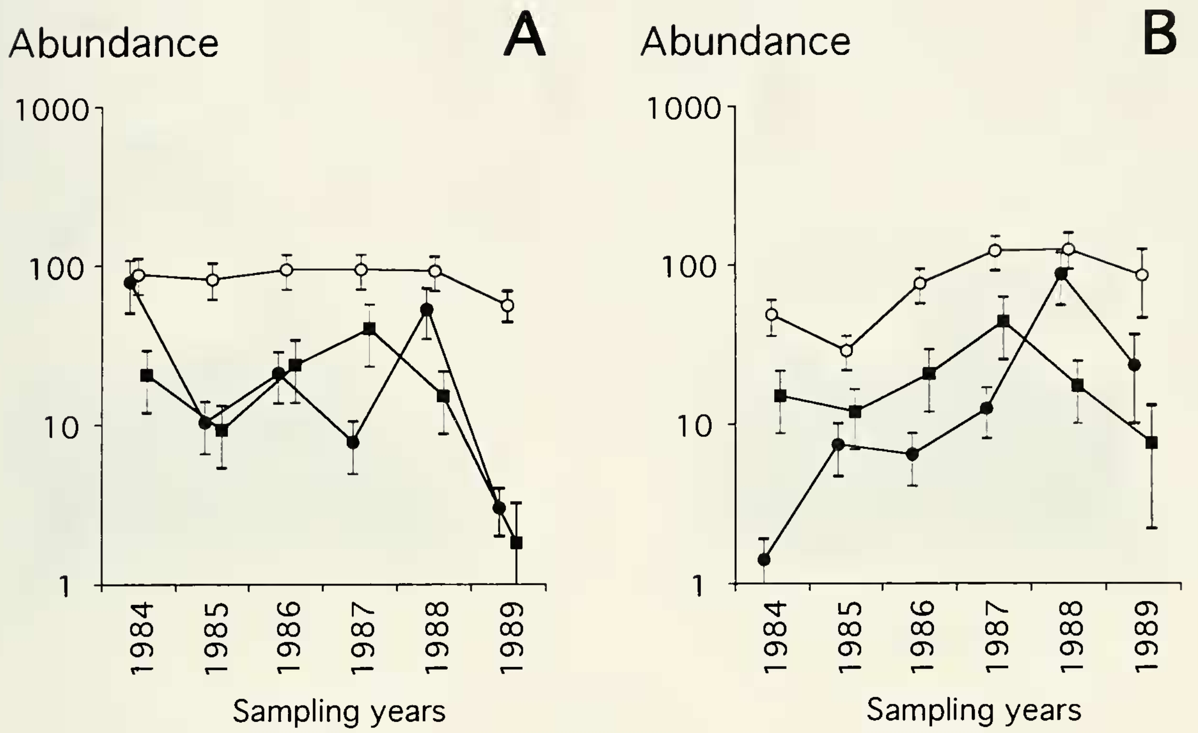

FIG. 6

Long-term changes in the abundance (individuals/cm^2; average ± standard error) of moss-dwelling rotifers, nematodes and tardigrades in area 1 (A) and area 2 (B). Samples were taken every March between 1984 and 1989. Error bars (except 1989) denote estimated standard errors based on values given in tab. 1 (rotifers: ●; nematodes: ○; tardigrades: ■).

1). The abundance of nematodes was extremely stable in area 1 between 1984 and 1988, whereas in area 2 nematode numbers increased constantly between 1985 and 1988. Tardigrade numbers decreased slightly between 1984 and 1985, and to a greater extent between 1987 and 1989, after a prominent peak in March 1987. Their abundance varied similarly at both microsites ($r_s = 0.94$, $p < 0.05$), and showed also a similar temporal pattern to the abundance of nematodes in area 1 (tardigrades area 1: $r_s = 0.93$; tardigrades area 2: $r_s = 0.99$; $p < 0.05$).

6. Long-term variation in species composition

Nematodes

In area 1 (fig. 7A) the long-term variation in nematode numbers was less pronounced than in area 2. Prominent taxa were *P. intermedia*, *C.* cf. *andrassyi*, Plectidae sp. and *G. villosa*. Furthermore, *Aphelenchoides* sp. 5, *T. auriculatus* and *P.* cf. *parietinus* were found in almost all samples. All these taxa were also recorded in preliminary samples (1982), as well as in the samples used to describe the seasonal variation of the aquatic fauna (see fig. 3).

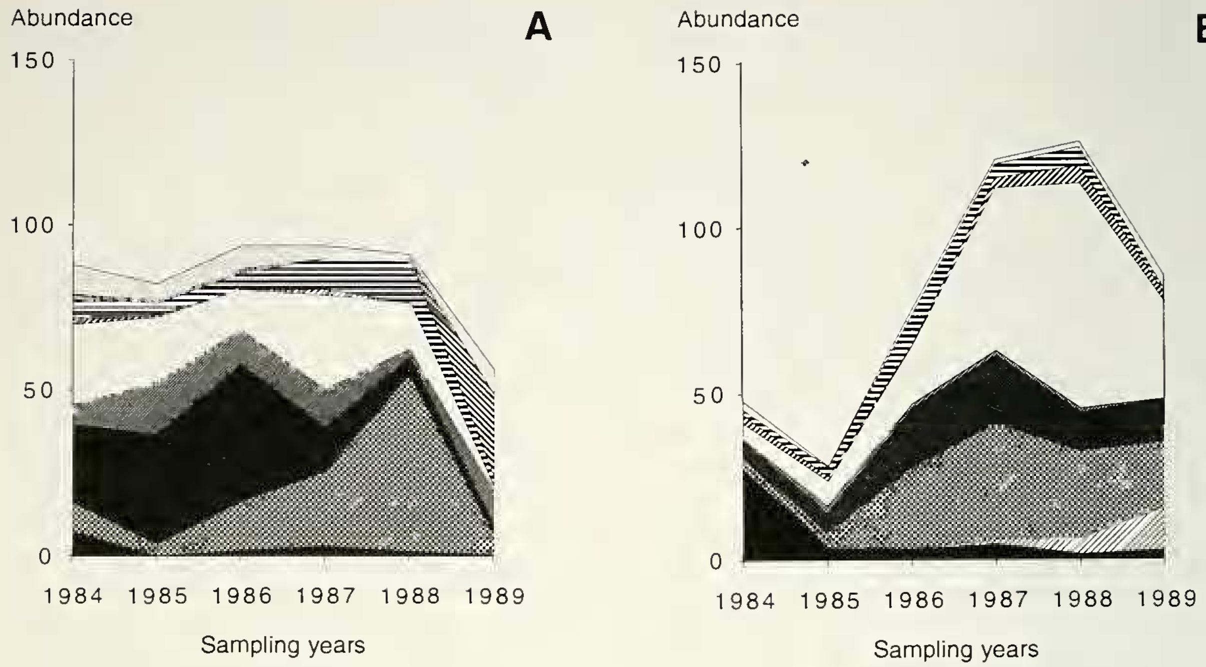

FIG. 7

Long-term changes in abundance (individuals/cm^2) of moss-dwelling nematode taxa in area 1 (A) and area 2 (B). Samples were taken every March between 1984 and March 1989. For graphical patterns see fig. 3.

Tardigrades

Long-term changes in tardigrade numbers were nearly identical (fig. 8) with almost the same number of individuals (area 1: 554, area 2: 583). However, slight differences exist in the qualitative composition. While in area 1 *H. oberhaeuseri* and/or *M. persimilis* dominated throughout the study, in area 2 *Hypsibius convergens* Urbanowicz s.l. became the dominant species after March 1986 (fig. 8B). Six tardigrade species were encountered in area 2, including the five species recorded in area 1 (*Hypsibius pallidus* Thulin occurred exclusively in area 2). Some species formerly found in the study of short-term dynamics were exceedingly rare (i.e. *M. richtersi* and *H. pallidus*) or were not detected (i.e. *I. prosostomus*).

Preliminary samples (August 1982) and the samples of August 1983 revealed the following species in area 1: *M. persimilis*, *M. hufelandi* and *H. oberhaeuseri* (*H. convergens* s.l. was only detected in 1983). In area 2, only two specimens were extracted in 1982 (i.e. *H. convergens* s.l. and *H. pallidus*), while all the common species (other than *H. convergens* s.l.) were found in 1983.

7. LONG-TERM VARIATION IN SPECIES RICHNESS

The long-term variation in species richness (fig. 9) was of the same range as its annual fluctuation (fig. 5). Nematode communities were constantly richer in species than tardigrade communities. Area 1 was characterised by a more diverse nematode

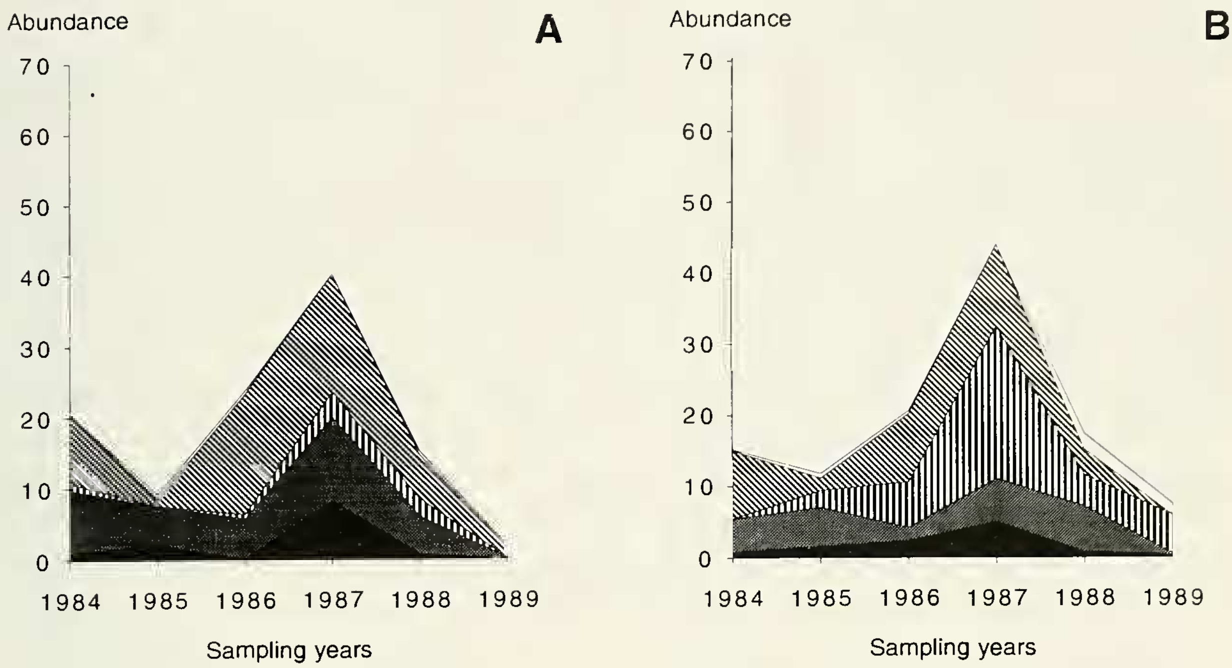

FIG. 8

Long-term changes in the abundance (individuals/cm^2) of moss-dwelling tardigrade taxa in area 1 (A) and area 2 (B). Samples were taken every March between 1984 and 1989. For graphical patterns see fig. 4.

fauna than area 2, whereas no significant differences were found for tardigrades (fig. 9). Preliminary samples taken in August 1982 revealed similar conditions.

DISCUSSION

The analysis of population fluctuations of aquatic animals is part of an extended study (STEINER 1994a, b, 1995a, b) investigating the suitability of moss-dwelling invertebrates as indicators of air pollution. An observation period of more than seven years allowed the estimation of the stability of nematode and tardigrade communities over several generations. Note that the life span of free-living nematodes and tardigrades varies from several days to 30 months (MORGAN, 1977; NICHOLAS, 1984). Knowledge about the seasonal changes of these communities helped to define the sampling plan used in an extensive synecological study concerning the moss-dwelling aquatic fauna (STEINER 1994a, b).

To minimise disturbance caused by repeated destructive sampling, a relatively small sample size was chosen in the present study (chapter Material and methods, Section 2). Therefore, the accuracy of population estimates was relatively low (tab. 1), and temporal fluctuations in population size are not necessarily significant. The amount of intersample variation was of the same order as obtained by HALLAS & YEATES (1972)

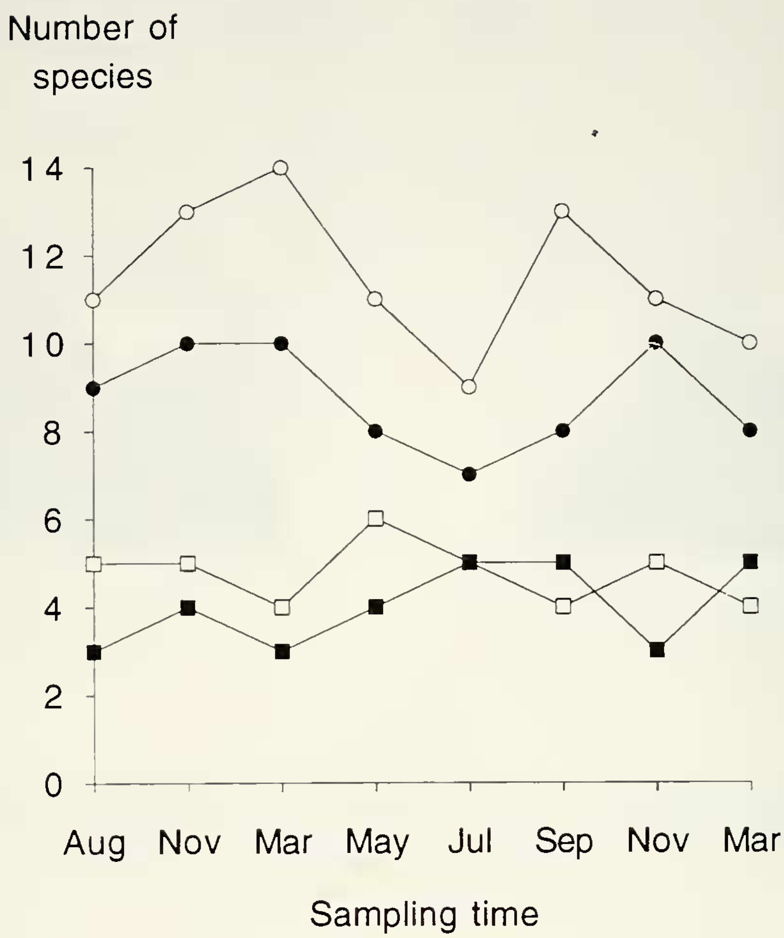

FIG. 9

Long-term changes in species richness of moss-dwelling nematodes and tardigrades in area 1 and area 2. Samples were taken every March between 1984 and 1989 (nematodes in area 1: ○, in area 2: ●; tardigrades in area 1: □, in area 2: ■).

in an extensive study on the dynamics of soil-dwelling nematodes and tardigrades. The peak in the abundance of both nematodes and tardigrades in May (figs. 3, 4) parallels findings by ZULLINI (1971) and YEATES (1972) for nematodes and MORGAN (1977) for tardigrades. These authors, however, noted a second peak in autumn. The lack of a second population peak in autumn (fig. 1) could be caused by the weather in summer, that differed from the long-term average by lower levels of precipitation and higher temperatures (July 1983 and 1984: 22.1 and 18.1 °C). Complying with findings by ZULLINI (1971) the abundance of nematodes was negatively related to temperature (fig. 2). The dependence on temperature is probably associated with the seasonal pattern of the microbial biomass. As indicated by WYNN-WILLIAMS (1980, cited in DAVIS, 1981), there is a microbial blooming in spring due to high availability of dissolved organic compounds released from moss cells ruptured by freezing and thawing action. This could explain the sharp increase in bacterial feeding Plectidae (predominantly unidentified first larval instars) between March and May (see fig. 3A). The decrease in tardigrade numbers at high temperatures (fig. 2B) could be due to depletion of the algal food source (MARCUS, 1929).

Differences in the long-term abundance patterns of rotifers and nematodes from neighboring microsites suggest that factors other than the weather regulate these populations. According to ZULLINI (1970), the population dynamics of moss-dwelling nematodes are influenced by micro-environmental conditions. For example, the two microsites of the present study could have been subjected to a different succession in moss species, associated microflora and fauna. Predators could also determine the abundance of the aquatic fauna. Although there was no significant correlation between the abundance of moss-dwelling predators (including nematodes, tardigrades and mites) and other aquatic animals, the influence of predator-prey interactions in shaping the communities can not be excluded. The lack of knowledge on the food web, the exclusion of predatory protozoans and endoparasitic or invertebrate-trapping fungi (see MORGAN, 1977), as well as the limited sampling effort disable to define the role of predators at the two microsites.

Most nematode and tardigrade taxa were recorded throughout the year, as noted by ZULLINI & PERETTI (1986) for moss-dwelling nematodes. Differences in species numbers were caused by low density species, that sometimes escaped detection with the current sampling methods. The most favourable sampling season, referring to time costs, is between September and March. During this period, the abundances were low to intermediate as compared to the whole annual cycle (fig. 1), but the number of species was relatively high (fig. 5). The low dependence of species richness on abundance suggests that sampling effects were unimportant for the assessment of local species composition.

Five main characteristics are detected in the long-term variation of nematode and tardigrade communities. First, the more abundant species were always present. Second, rare taxa (other than *Panagrolaimus* sp.) were usually found only in low numbers throughout the study period. For example *Eudorylaimus* cf. *carteri* (Bastian), *Anaplectus granulosus* (Bastian) and *Hypsibius pallidus* occurred in very low numbers (≤ 4 individuals) in four of the six samples taken between 1984 and 1989. Third, in some species long-term population changes seem to be superimposed upon the basic annual cycle. For example *Geomonhystera villosa* (figs 7A and B) and *Chiloplectus* cf. *andrassyi* (fig. 7B) steadily increased in numbers between 1985 and 1988, while *Aphelenchoides* sp. 5 declined after a peak in 1984 (see also fig. 3B) and subsisted at low levels in subsequent samples. Fourth, consistent differences exist in the qualitative composition of the communities of the two microsites, although the moss species were identical and the two sites were only two meters apart. Nine of the less abundant nematode species were exclusively found in area 1, while only four species (i.e. the tardigrade *H. pallidus* and the nematodes *Theristus* sp., *Ceratoplectus armatus* (Bütschli) and *Teratocephalus terrestris* (Bütschli)) were restricted to area 2. Fifth, no evidence exists for substantial long-term changes in species composition, and only the predominant species differed with time. Thus, species richness remained almost unchanged between 1982 and 1989, and seems to be characteristic for a given microsite.

CONCLUSIONS

The following conclusions seem justified from the seasonal and long-term analysis: (1) Moss-inhabiting nematodes and tardigrades exhibited pronounced seasonal population fluctuations. (2) Differences in the qualitative composition of neighboring microsites agree with findings of MORGAN (1977) and ZULLINI (1970) for tardigrade and nematode populations, respectively. This small scale variation reflects the importance of micro-environmental conditions for the moss-dwelling aquatic fauna. (3) Consistent differences in the qualitative composition of neighbouring microsites emphasise the necessity to investigate several moss cushions to characterise a site by its microfauna. (4) Most species were found throughout the year. Therefore, assessment of the qualitative composition of moss-dwelling nematode and tardigrade communities is not bound to a certain season. (5) Species richness and species composition are typical features of a given microsite over several years, whereas the dominance pattern during any year and/or season may be quite atypical of the locality. (6) Referring to time costs, the most effective sampling period for the assessment of the qualitative composition of the moss-dwelling aquatic fauna is between September and March. (7) The observed long-term stability of nematode and tardigrade communities, along with their sensitivity to pollution (STEINER 1994b), show that the moss-dwelling aquatic fauna can be used as an ecological system to predict effects of air pollution.

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